



Inbreeding produces trade-offs between maternal fecundity and offspring survival in a monandrous spider



Zhanqi Chen ^a, Evan L. Preisser ^b, Rong Xiao ^a, Jian Chen ^a, Daiqin Li ^c, Xiaoguo Jiao ^{a,*}

^a Center for Behavioral Ecology & Evolution, Hubei Collaborative Innovation Center for Green Transformation of Bio-Resources, College of Life Sciences, Hubei University, Wuhan, China

^b Biological Sciences Department, University of Rhode Island, Kingston, RI, USA

^c Department of Biological Sciences, National University of Singapore, Singapore

ARTICLE INFO

Article history:

Received 23 February 2017

Initial acceptance 27 March 2017

Final acceptance 31 July 2017

MS. number: 17-00189R

Keywords:

courtship
fecundity
fitness
inbreeding avoidance
mate discrimination
mating
monandrous
spider

Offspring born to related parents often have lower fitness than those born to unrelated parents, a phenomenon termed inbreeding depression. While many species have been shown to rely on pre- and/or postcopulatory mate choice to avoid inbreeding, such research has focused largely on polyandrous rather than monandrous species. The absence of postcopulatory mate choice in monandrous species suggests that precopulatory mate choice should play a more important role in inbreeding avoidance. We used a monandrous wolf spider, *Pardosa astrigera*, as a model system to investigate whether (1) male spiders respond differently to sibling and nonsibling females; (2) female spiders respond differently to sibling versus nonsibling males; and (3) inbreeding affects females and their offspring. Male courtship behaviour was similar for sibling and nonsibling females; although females were less likely to mate with siblings, over half did mate successfully with them. Sibling-mated females produced fewer offspring from the first egg sac and fewer total offspring, but inbred offspring survived longer in a range of environments than their outbred counterparts. This suggests that the fitness costs of reduced fecundity in sibling-mated females may be offset by higher offspring survivorship. Our results highlight the importance of considering both parent and offspring fitness when addressing the costs of inbreeding, and are the first to document the impact of inbreeding on sexual behaviour and reproductive fitness in a monandrous spider.

© 2017 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Inbred individuals are often less fit than outbred individuals, a phenomenon generally resulting from increased homozygosity at loci carrying rare deleterious recessive alleles or exhibiting overdominance (Charlesworth & Charlesworth, 1987; Lynch, 1991). The fitness costs of inbreeding have been documented in an array of taxa, and exert a strong selective pressure on both mating and reproductive strategies (Bateson, 1982; Escobar et al., 2011; Muller & Muller, 2016; Szulkin, Stopher, Pemberton, & Reid, 2013). The impact of inbreeding on offspring can be altered by the surrounding environment. Varying environmental conditions, for example, can cause stress and often exacerbate the effects of inbreeding (Armbruster & Reed, 2005). These stressors can include suboptimal diets (Fox & Reed, 2011; Freitak, Bos, Stucki, & Sundstrom, 2014) and variation in temperature (Fox & Reed, 2011; Kristensen, Barker,

Pedersen, & Loeschcke, 2008), and are widely recognized to exacerbate the fitness costs of inbreeding.

An array of mechanisms has evolved for avoiding inbreeding and/or reducing its fitness costs (Firman & Simmons, 2008; Pusey & Wolf, 1996; Ruch, Heinrich, Bilde, & Schneider, 2009). Prior to breeding, sex-biased dispersal from natal habitats decreases inbreeding risk in some species (Keane, 1990; Pusey & Wolf, 1996; Smith, Su, Berger-Tal, & Lubin, 2016), while other species prefer to mate with unrelated partners (Fischer, Karl, Heuskin, Janowitz, & Dotterl, 2015; Thomas & Simmons, 2011; Whitehorn, Tinsley, & Goulson, 2009). The recognition and avoidance of related individuals requires chemical or other cues that are indicative of relatedness (Firman & Simmons, 2008; Pusey & Wolf, 1996; Ruch et al., 2009). In insects, for instance, both mate recognition and premating preference are affected by cuticular hydrocarbons (CHCs; Geiselhardt, Otte, & Hilker, 2009; Thomas & Simmons, 2011) and other compounds (Chuine, Sauzet, Debias, & Desouhant, 2015; Herzner, Schmitt, Heckel, Schreier, & Strohm, 2006). The CHC profiles of several chrysolid beetle species, for example, affect

* Correspondence: Xiaoguo Jiao, College of Life Sciences, Hubei University, Youyi Street 368 Wuchang, Wuhan 430062, Hubei, China.

E-mail address: jjiaoxg@hubu.edu.cn (X. Jiao).

mate choice and facilitate outbred mating (Geiselhardt et al., 2009). Even if inbreeding does occur, its impact in polyandrous species can be reduced via postcopulatory mechanisms in which differential fertilization success depends on patterns of relatedness rather than intrinsic male quality (Bretman, Wedell, & Tregenza, 2004; Firman & Simmons, 2008; Fitzpatrick & Evans, 2014).

Research exploring inbreeding avoidance has primarily addressed polyandrous species, organisms capable of employing both pre- and postcopulatory mate choice strategies (Cornell & Tregenza, 2007; Firman & Simmons, 2008; Tregenza & Wedell, 2002; Welke & Schneider, 2009). This focus reflects the genetic benefits likely to be necessary for polyandry to evolve in species where females derive little or no material benefit from males (reviewed in Simmons, Beveridge, Wedell, & Tregenza, 2006). In contrast, inbreeding in monandrous species has received far less attention. Because monandrous females only mate once within a single reproductive episode, inbreeding avoidance must occur via precopulatory mechanisms (Hosken, Stockley, Tregenza, & Wedell, 2009). In situations where inbreeding is costly, monandrous species may thus possess especially effective precopulatory barriers. The strength of these barriers may, however, vary by sex: because male fitness is relatively unaffected by inbreeding, males should be more tolerant of sibling matings than females (Duthie, Lee, & Reid, 2016).

The wolf spider *Pardosa astrigera* is widely distributed in East Asia. Male courtship consists of two distinct behaviours, body shaking and foreleg raising (Wu, Jiao, & Chen, 2008). Olfaction plays a key role in male courtship. Males initiate courtship in response to pheromones associated with female dragline silk, and males can distinguish silk cues from individuals differing in sex and mating status (Xiao et al., 2015). While female *P. astrigera* are monandrous, the polygynous males can copulate with as many as five virgin females at 24 h intervals (Jiao et al., 2011; Wu et al., 2008). While inbreeding depression has not previously been addressed in this species, previous research into its courtship and mating behaviour make it an ideal model system for addressing such questions.

We report work investigating inbreeding avoidance through courtship behaviour and the impact of inbreeding on reproductive output and offspring survival in the monandrous wolf spider *P. astrigera*. We compared male courtship behaviours in response to dragline silk of sibling and nonsibling females to test for male precopulatory kin discrimination. We also conducted nonchoice mating experiments to compare the likelihood of sibling and nonsibling mating. In addition, we measured postmating female reproductive output (both number and size of offspring) to determine the cost of inbreeding for female fitness. Finally, we compared the survival of inbred versus outbred offspring across a range of temperatures. We predicted that strong precopulatory barriers exist to sibling mating, that these barriers are stronger in females than in males, that inbreeding reduces both maternal and offspring fitness, and that higher temperatures increase the impact of inbreeding on the offspring.

METHODS

Study Species and Maintenance

Subadult *P. astrigera* of the overwintering generation were collected in April 2012 from Ma'anshan Forest Park, Wuhan, Hubei Province, China. Spiders were housed individually in opaque Plexiglas enclosures (5.0 × 5.0 cm and 7.5 cm high) at 25 ± 0.5 °C with 60 ± 10% relative humidity and on a 14:10 h light:dark cycle. Spiders were supplied with water ad libitum and fed every 3 days with a mixture of *Drosophila melanogaster* and mosquitoes (Culicidae). Individuals were checked daily for subadult moulting in order to

determine the exact date of adulthood. We used randomly selected adult spiders to create the 10 male:female pairs used to generate 10 families. Mated females were maintained as above. We randomly selected and reared 30 spiderlings from each egg sac; each spiderling was reared individually in a glass tube (1.5 cm diameter). Spiderlings were supplied with water ad libitum and fed every 2 days with a mixture of *D. melanogaster* and mosquitoes. Once the spiders matured, similarly sized females in their third day of adulthood were selected for silk collection and/or behavioural trials. All spiders were virgin and used only once; all adult spiders, except for those females whose life span was measured (details below) were released following their involvement in the experiment.

Experiment 1: Male Responses to Sibling/Nonsibling Female Silk

Silk was collected by placing each female in a 9 cm diameter glass petri dish lined with filter paper (15 cm diameter; Double Ring brand, Hangzhou, Zhejiang, China) for 12 h. All females were starved for 12 h beforehand to reduce faecal contamination. All silk was used within 18–24 h after its collection, during which silk-borne spider cues do not degrade under natural conditions (Baruffaldi, Costa, Rodriguez, & Gonzalez, 2010; Costa, Curbelo, & Perez-Miles, 2015).

We randomly selected similarly sized virgin males ($N = 65$, 5–7 individuals per family) aged 5–10 days postmaturation and assigned each male to one of the two female silk stimulus treatments. Male body size did not differ significantly between treatments ($t_{61} = 0.75$, $P = 0.45$). Thirty-three males were exposed to silk from a female in the same family (sibling), and 32 to silk from a female from a different family (nonsibling); silk from a given female was only used for one male.

Behavioural trials were carried out in a cylindrical glass container open at both ends (10.5 cm diameter, 12 cm length). After the cylindrical glass container was placed on the silk-covered filter paper, a single male was gently introduced onto the stimulus filter paper with a glass tube from above and its courtship behaviour videotaped (HDR-CX580E Sony video camera) for 5 min. We chose this cutoff period because preliminary experiments revealed that male spiders exposed to silk either began courtship rapidly (within 2 min) or never engaged in courtship behaviour (Roberts & Uetz, 2004). Each arena was cleaned after each trial with 70% ethanol and left to air dry. Videos were analysed using Observer v. 4.1 (Noldus Information Technology, Wageningen, The Netherlands), a software package for behavioural data analysis. Based on work reported in Wu et al. (2008), the following courtship behaviours were analysed: (1) time to the start of body shaking and (2) foreleg raising and (3) the number of body shakes and (4) foreleg raises per min.

Data from all trials were analysed to determine whether the likelihood of courting behaviour was affected by female relatedness. For analysis of specific courtship behaviours, data from trials in which such behaviours did not occur within 5 min were excluded from analysis.

Experiment 2: Male and Female Response to Siblings and Nonsiblings

We paired individual virgin females ($N = 120$; 12 spiders from each family) in their third day of adulthood with individual virgin males 5–10 days into adulthood; 60 male–female pairs were siblings and 60 were nonsiblings. All spiders belonged to one of the 10 families. We recorded behavioural data on male courtship as per experiment 1, and whether mating occurred within 30 min. Data for replicates in which no mating occurred were used to analyse

Download English Version:

<https://daneshyari.com/en/article/5538299>

Download Persian Version:

<https://daneshyari.com/article/5538299>

[Daneshyari.com](https://daneshyari.com)